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Foraging Locations of Double-crested Cormorants on Western Lake Erie: Site Characteristics and Spatial Associations with Prey Fish Densities

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ABSTRACT. *Radio-tagged double-crested cormorants* (Phalacrocorax auritus) *nesting on Middle Island, Ontario and unmarked cormorants in the western basin of Lake Erie were monitored in 1999. Radio-tagged cormorants were located by aircraft and by boat along regular survey routes. In addition, foraging flocks of radio-tagged and unmarked cormorants were located during the boat surveys. Approximately 79% of foraging radio-tagged individuals, and approximately 65% of all foraging flocks were observed within 2.5 km of shore. These percentages were greater than expected, based on the percentage of the area of water within 2.5 km of shore. All size classes of flocks examined were found more frequently than expected on water ≤ 10 m deep. Trawling data collected annually from 1988 to 1999 during the month of August were used to determine the historical distributions of the four fish species found to comprise the majority of the diet of cormorants in the area. August corresponded to a period when there is maximal overlap in the diets of cormorants and walleye* (Stizostedion vitreum) *in the area and when the number of foraging cormorants in the area is large. Flocks of cormorants of all size classes examined were not found proportionately more in regions that contained higher than the historical median annual catches of any of the four prey species. These results, coupled with previous bioenergetics studies, suggest that the impact of cormorants on the fishery of the western basin of Lake Erie is localized with respect to depth and distance from shore.*

INDEX WORDS: Phalacrocorax auritus, *cormorant, prey fishes, Lake Erie, radiotelemetry, foraging locations.*

INTRODUCTION

Populations of double-crested cormorants (*Phalacrocorax auritus*, hereafter: cormorant) have increased dramatically in many parts of North America over the last 20 years (Hatch 1984, Vermeer and Rankin 1984, Chapdelaine and Bédard 1995, Tyson *et al.* 1999), including the Great Lakes (Ludwig 1984, Price and Weseloh 1986, Weseloh *et al.* 1995). On Lake Erie, for example, 87 cormorant nests were recorded in 1979 and 13,271 nests were recorded in 2000 (Weseloh *et al.* 1995, Shieldcastle and Martin 1999, and Weseloh *et al.* 2002). Cormorants are piscivorous, foot-propelled pursuit divers (Ashmole 1971, Cooper 1986, Wanless and Harris 1991, Watanuki *et al.* 1996). Many sport anglers and commercial fishers on the Great Lakes are concerned that cormorants directly deplete stocks of game fish such as walleye (*Stizostedion vitreum*), yellow perch (*Perca flavenscens*), and smallmouth

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bass (*Micropterus dolomieu*) or remove a disproportionate amount of prey biomass that supports predator fish populations (Ross and Johnson 1995, Burnett *et al.* 2002, Johnson *et al.* 2002, Lantry *et al.* 2002). Concern for the loss of fish to cormorants in Lake Ontario, for example, has resulted in incidents of illegal population control in 1993 and 1998 (Ewins and Weseloh 1994, New York Department of Environmental Conservation unpublished data).

Diet and foraging studies in the Great Lakes suggest that cormorants are opportunistic foragers that eat mostly small prey fish, such as young-of-the year and yearling gizzard shad (*Dorosoma cepedianum*), emerald shiner (*Notropis atherinoides*), freshwater drum (*Aplodinotes grunniens*), alewives (*Alosa pseudoharengus*), and sticklebacks (*Eucalia inconstans*) (Craven and Lev 1987, Hobson *et al.* 1989, Ross and Johnson 1995, Neuman *et al.* 1997, Bur *et al.* 1999, Trapp *et al.* 1999). Most of these species have little sport or commercial value (Bur *et al.* 1999). Further, bioenergetics studies (Madenjian and Gabrey 1995) suggest that cormorants remove less than 2% of the annual consumption of prey fish by the walleye population in western Lake Erie. Madenjian and Gabrey's (1995) bioenergetics model did not include the contributions of individual fish species in the diets of cormorants. However, cormorants consume large quantities of smallmouth bass and yellow perch in the waters near Little Galloo Island in Lake Ontario (Burnett *et al.* 2002, Johnson *et al.* 2002, Lantry *et al.* 2002).

Neuman *et al.* (1997) emphasized the importance of understanding the spatial and temporal aspects of cormorant foraging relative to those of the prey species. If abundance of prey fishes limits foraging activity of cormorants, then one may expect that the locations of foraging cormorants correspond with relatively high abundances of prey fishes. The objectives of this study were to (1) determine the locations of foraging flocks of cormorants in a section of the western basin of Lake Erie, (2) estimate the foraging range of cormorants from a nesting colony, and (3) determine if there is a spatial association between the foraging locations of cormorants and the historical distributions of their main prey fishes in the study area. To satisfy objective (3) this study used 12 years of prey fish data collected during the time interval in which the diets of cormorants and walleye overlap most (Bur *et al.* 1999). Accomplishment of these objectives, coupled with available diet data, could then be used to develop a detailed bioenergetics model to estimate annual consumption by cormorants and their potential impacts on populations of prey and predatory game fishes. Baseline data in the form of preferred foraging areas could be valuable information for resource managers on Lake Erie and other lakes impacted by cormorants. Associations between foraging areas and the historical distributions of fishes may further assist in estimating the impact of cormorants on the fishery of Lake Erie.

STUDY AREA

The study was conducted in the western basin of Lake Erie, between 41° 30′ and 41° 54′ N latitude and 82° 34′ and 82° 55′ W longitude (Fig. 1). The study area included approximately 1,197 km^2 of water in Ohio, USA and Ontario, Canada. The size of the survey area was established to encompass an area that would include the maximum documented foraging range of cormorants (Palmer 1962, Hobson *et al.* 1989, Wanless *et al.* 1991, Custer and Bunck 1992). Approximately 60% of the water in the study area was relatively shallow ($\leq$ 10 m deep), based on volume and bathymetry data (National Environmental Satellite, Data, and Information Service [NESDIS] 1999). Low-water datum depth varies from approximately 0.25 m surrounding reefs and shorelines to approximately 16 m in pelagial zones. Numerous islands and reefs characterize this portion of Lake Erie. The study area included Pelee, Kelleys, and South Bass islands (Fig. 1), the three largest islands on Lake Erie. The study area also included Middle Island and East Sister Island, both of which had more than 3,400 nesting pairs of cormorants in 1999.

Foraging activity of radio-tagged adult cormorants nesting on Middle Island, Ontario was monitored (Fig. 1). The number of cormorant nests on Middle Island increased from 3 in 1986 to 3,479 in 1999 to 5,202 in 2000 (Weseloh *et al.* 2002 and D.V. Weseloh, Canadian Fish and Wildlife Service unpublished data). Middle Island has an area of approximately 0.21 km^2 and had had no permanent residents or even regular summer residents since 1979. The island was almost entirely wooded, except for a rock and boulder beach approximately 10 m wide that surrounded the island. Trees 10 to 15 m in height served as cormorant nest sites. Trees and heavy herbaceous growth dominated the vegetation on the island.

METHODS

Radio-tagging Cormorants

Twenty cormorants were captured with Victor #3 padded-jaw leghold traps (King *et al.* 1998) placed

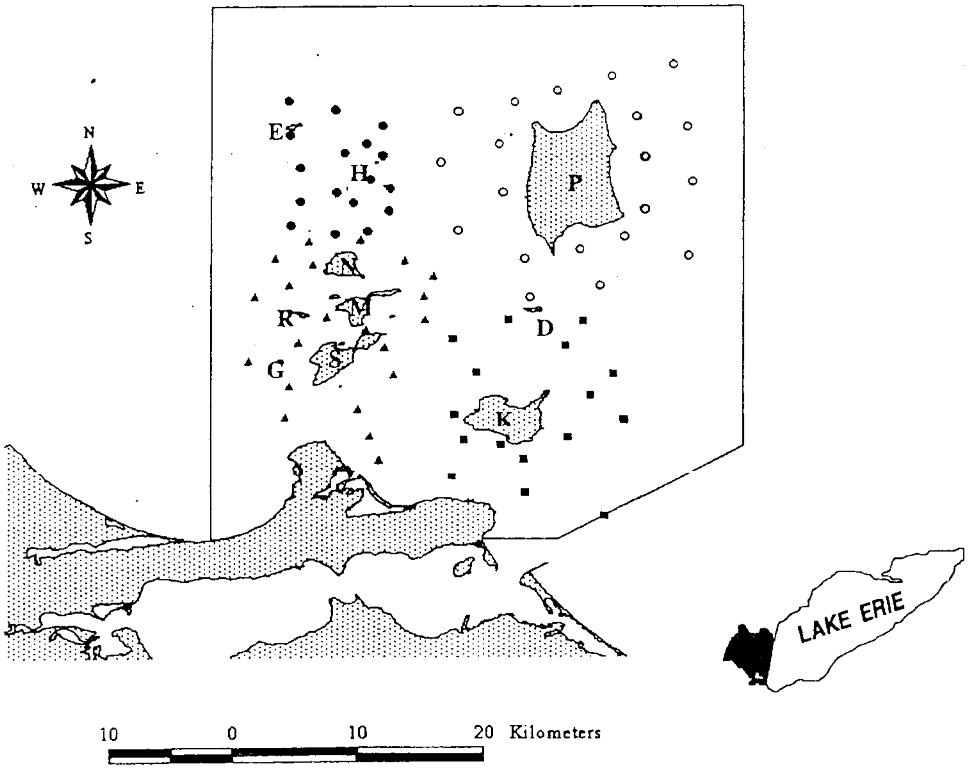


FIG. 1. Location of the study area in western Lake Erie (enlarged, with respect to Lake Erie). Surface tracking of radio-tagged cormorants was conducted at 74 stations along four census routes, each route represented by a unique shape. The solid line indicates the boundaries of the study area. Symbols: ▲ = Bass Islands route (21 stations), ● = Chicken Islands route (17 stations), ■ = Kelleys Island route (16 stations), ○ = Pelee Island route (20 stations), D = Middle Island, E = East Sister Island, G = Green Island, H = Hen Island, K = Kelleys Island, M = Middle Bass Island, N = North Bass Island, P = Pelee Island, R = Rattlesnake Island, S = South Bass Island.

at the edge of nests in trees on Middle Island. These nests were typically 5 to 7 m aboveground. The factory chains on the traps were replaced with a 20-cm length of 3.7-mm aircraft cable and a 30-cm shockcord to minimize injury to captured birds. The coil springs were replaced with weaker Victor #1.5 Soft-catch coil springs (King *et al.* 1998). A transmitter (Advanced Telemetry Systems, Inc., Isanti, Minnesota) with a unique frequency (between 164.104 and 164.392 MHz) was attached to the back of each cormorant, using techniques described by Morris and Black (1980) and Belant *et al.* (1993). The antenna of each transmitter was directed posteriorly. The transmitter was attached to each cormorant with an adjustable backpack harness made of 6-mm wide Teflon ribbon (Belant *et al.* 1993). The ends of the ribbon were sewn together with cotton thread so that the harness would maintain a stable position yet not hinder movement. The entire radio package weighed approximately 25 g, or about 2% of the mass of an adult cormorant. Trapping was conducted in May and June 1999, and monitoring was conducted from May through October 1999. One radio-tagged cormorant died due to unknown causes, and a transmitter fell off of another cormorant during this study. Therefore, data for only 18 individuals were included in the analyses. Radiotelemetry data were used to determine distances from the colony and from nearest shore at which cormorants foraged. Data from radio-tagged individuals were combined with data from unmarked individuals to test hypotheses about foraging locations with respect to distance from shore, depth, and historical distributions of prey fishes.

Surface Observations

All geographical positions were determined with a Garmin GPS-III Plus Personal Navigator (Garmin Corporation, Olathe, Kansas), set at datum WGS-84. This instrument has an advertised accuracy of ±100 m. Surface observations were made from a 7.3-m Boston Whaler. Seventy-four monitoring stations were established at fixed coordinates along four routes within the survey area (Fig. 1). The amount of shoreline and area of open water to be scanned was different for each route. Trees, rocky outcrops, structures built by humans, and radio communications on the shorelines of islands and reefs provided sources of interference for the signals from the transmitters. The number of stations on each route was adjusted to accommodate these sources of interference and shoreline. However, the amount of time (approximately 4 hr) required to complete monitoring was approximately the same for each route.

For each route there were two practical sequences in which to visit the stations. For any given day, this sequence was determined randomly. Six replicates of each census route were completed between 15 July and 28 September 1999. All surface observations were conducted under the following conditions: average wave height ≤ 1 m, wind speed ≤ 25 km/hr, and visibility > 4 km. Data collected during overcast conditions or precipitation were not included.

At each station, radio-tagged individuals were located with a hand-held Yagi antenna and receiver (model R2100, Advanced Telemetry Systems, Inc., Isanti, Minnesota) using standard telemetry techniques (Mech 1983). Each frequency was scanned for 8 sec from the bow of the boat. When a radio-tagged cormorant was detected, its location was determined by piloting the boat toward the signal. When there was visual confirmation of the individual and transmitter, the coordinates were recorded as determined by the GPS unit. The activity of the cormorant (foraging, flying) was recorded and the size of the flock associated with the radio-tagged individual was estimated.

While tracking at each station and traveling between stations, the number of unmarked and radio-tagged cormorants observed on the water was recorded. It was assumed that cormorants on the water were foraging. Cormorants typically alternate relatively short periods of diving with relatively long periods of resting on the water or on shore (Wanless *et al.* 1991). When a foraging flock was sighted, the location of the center of the flock was estimated visually. The boat was then piloted at idle speed (≤ 4 km/h) to that position, and the coordinates as determined by the GPS unit were recorded. This technique typically minimized flushing and redistribution of cormorants. The same observer (MAS) located all flocks and counted the number of cormorants in those flocks. Foraging flocks were tracked and searched between 0700 and 1100 EDT, the peak foraging period of cormorants (Lewis 1929; Mendall 1936; Dunn 1975; M. Bur, USGS, unpublished data). Remote, continuous monitoring of radio-tagged individuals from a datalogger (Model D5041 with a 12-v car battery, Advanced Telemetry Systems, Inc., Isanti, Minnesota) located on Middle Island revealed that cormorants spent approximately 39% of this time period within 1 km of Middle Island (M. Stapanian and M. Bur, USGS, unpublished data).

Aerial Surveys

Thirteen aerial surveys were flown between 1 July and 14 October 1999 from a twin-engine Partenavia 68 aircraft at an altitude between 150 m and 215 m above ground level and a cruising speed between 175 km/hr and 200 km/hr. Aerial surveys were conducted between 0700 and noon EDT. The aircraft was equipped with a Yagi antenna fixed to the aircraft and a receiver (model R2100, Advanced Telemetry Systems, Inc., Isanti, Minnesota). The aerial crew consisted of a pilot and an observer. Tracking on each survey began over Middle Island, then continued along North-South transects in the study area east of Middle Island. Transect lines were separated by approximately 0.8 km. Each frequency was scanned for 8 sec. When this set of transects was completed, the aircraft returned to Middle Island and repeated the search of the island. Tracking resumed along North-South transects in the study area west of Middle Island. When a radio-tagged individual was detected, the aircraft's speed and altitude were decreased to obtain reliable coordinates for the location of the cormorant. From the aerial surveys, only data for radio-tagged cormorants that were found on the water are reported.

The accuracy of locating radio-tagged cormorants on aerial surveys was evaluated by attaching a transmitter to a fixed object (marker buoy, tree, or dock support) and recording the coordinates with the GPS unit prior to each survey. The observer and the pilot were never informed of the locations of the transmitter or that the transmitter was not attached to a cormorant. The aerial surveys located this transmitter within approximately ±0.4 km of the coordinates originally recorded by the GPS unit (M. Stapanian and M. Bur, USGS, unpublished data).

For radio-tagged cormorants located from surface and aerial tracking, the distributions of the distances from Middle Island, distances from nearest shore, and depths were tested for normality with a Kolmogorov-Smirnov test. Kruskal-Wallis tests were used for hypothesis testing when the data were not distributed normally. A Kruskal-Wallis test was used for the null hypotheses that the median distances from nearest shore and from Middle Island were equal for radio-tagged cormorants recorded on aerial and on surface surveys. Standard regression techniques were used to test if the natural log of the distances from Middle Island changed during the study period for radio-tagged cormorants. In addition a Kruskal-Wallis test was used for the null hypotheses that the median depths and median distances from nearest shore for radio-tagged cormorants were equal to those for flocks of cormorants that did not contain radio-tagged individuals. Flocks were partitioned into four size classes: 1 to 10, 11 to 100, 101 to 1,000, and > 1,000 individuals. An analysis of variance (ANOVA) was used to test the null hypothesis that the mean depths of the foraging locations were equal for all classes.

Geographical Information Methods

Bathymetry data for the study area were obtained from NESDIS (1999). The areas of each 1-m depth contour were estimated using the Albers equal-area projection after clipping the bathymetry data to the study area in ArcView software (ESRI 1999). The coordinates of the foraging flocks and of the foraging radio-tagged cormorants were overlaid onto the bathymetry map of the study area. Depth was estimated from bathymetry maps, distance from nearest shore, and distance from Middle Island in ArcView using the equidistant conic projection.

The location of each foraging flock was classified as occurring in either "shallow" or "deep" water. "Shallow" water was defined in two ways: (1) ≤ 10 m, the approximate mean depth of the study area, and (2) ≤ 8 m, which represented approximately the upper limit of the shallowest depth quartile in the study area i.e., 28.4% of the study area was ≤ 8 m. Previous studies (Mendall 1936, Palmer 1962, and Custer and Bunck 1992) found that *P. auritus* preferentially foraged in waters < 10 m deep. The null hypothesis that foraging flocks of cormorants were recorded in equal proportions, based on area, in "shallow" and "deep" water was evaluated with a Chi-square test (df = 1). Separate analyses were performed for each of the four size classes of flocks and for all flock sizes combined. When expected values were less than 5 flocks, the null hypothesis was tested with a binomial distribution. Similarly, we tested the null hypothesis that foraging cormorants were recorded equally, based on area, at distances of ≤ 3 km from shore and ≤ 2.5 km from shore with the same techniques. These distances were selected because they were representative of the distances from shore at which Custer and Bunck (1992) recorded most foraging cormorants. Approximately 39.1% and 32.6%, respectively, of the area of the water in the study area was within 3.0 km and 2.5 km of shore. Standard correlation procedures were used to examine the relationship between the number of foraging flocks, irrespective of size, located within 3 km of islands and $\log_e$ of the areas of the islands nearest to those feeding flocks. In preliminary analyses, we found that the $\log_e$ transformation was reasonable for determining linear relationships. Further, log transformations of island areas have been commonly used in island biogeography studies, albeit typically for species richness models (MacArthur and Wilson 1967 and references therein). Discordancies in magnitude and trend were identified with Mardia's multivariate kurtosis (Mardia 1970, 1974; Garner *et al.* 1991; Stapanian *et al.* 1991).

Historical Distributions of Prey Fishes

Fish distribution was characterized within the study area with data collected from a bottom trawling survey that was conducted annually during the month of August from 1988 through 1999 by the Ohio Division of Wildlife (ODW) and the Ontario Ministry of Natural Resources (OMNR). Fish data for August were used because the composition of the diets of walleye and cormorants in western Lake Erie overlap most from August through October (Bur *et al.* 1999). Further, cormorant populations in the study area were high during mid- to late August because first-year birds were foraging by then (M.A. Stapanian, unpublished data). Twelve years of prey fish data were used because averaging the results over multiple years provided more robust distribution patterns than just the most recent year's data. In addition, spatial patterns of several fish species appear to persist from one year to the next (Scott and Gavaris 1985, Smith and Gavaris 1993).

The interagency trawling data are used primarily as an index of both percid and forage fish recruitment in the western basin of Lake Erie. Between 75 and 80 tows per year were conducted during the third week of August by OMNR and ODW throughout the western basin of Lake Erie. Tows were randomly stratified by depth (depth strata 0 to 3 m, 3 to 6 m, 6 to 9 m, and > 9 m) in trawlable areas. A subset of these trawl sites (n = 34) was in the study area and used for this analysis. All trawls were conducted during daylight hours, using a standard, flat bottom otter trawl with a 10.3-m headrope and 6.4-mm bar mesh in the cod-end. A single, 10-min tow was conducted at each of the sites in each year. Catches were sorted by species and age and enumerated.

For each fish species analyzed, catches were represented as catch per ha at each site and pooled within years. The effects of annual changes in abundance were accounted for by calculating, for each site, a percent rank of the total annual catch for all sites pooled,

$$\text{Percent Rank}_i = (R_{ij}/n_j) \cdot 100 \qquad (1)$$

where R_{ij} = rank of the ith observation in the jth year and n_j = number of observations in the jth year. This procedure standardized the catch per ha at each site within each year. Catch was standardized by number of sites sampled in a year because, due to technical difficulties, not all sites were sampled every year. The historical percent rank value of the catch was calculated at each of the 34 trawl sites as the geometric mean of the annual percent ranks across the 12-year survey period. These historical percent rank values indicated consistently "good" or "poor" catches across years at particular sites (regardless of year-class strength).

In order to construct contours of catch at any point in the sample region, a technique known as kriging interpolation (Cressie 1993) was used. Kriging interpolation is a geostatistical technique based on the theory of regionalized variables developed by Matheron (1963). The basic premise of kriging interpolation is that every unknown point (E $[x_i, y_i]$) can be estimated by the weighted sum of the known points. A grid of 50 by 50 points was laid over a map of the study area and estimates of mean percent rank were estimated for each grid node using the kriging equations with the linear variogram option in Surfer (Golden Software 1995) and data from the trawl survey. Each contour line was then interpolated for the quartiles (≤ 25%, 26 to 50%, 51 to 75%, and > 75%) of the historical percent rank data. The respective areas of the regions bounded by the quartile contours were calculated using the Albers equal-area projection in ArcView software (ESRI 1999). Each region bounded by the quartile contours was classified as either "high" catch (historical rank value ≥ median value) or "low" catch (historical rank value < median value) for each fish species.

Distribution maps were generated for age-0 gizzard shad, age-1 and older emerald shiner, age-1 freshwater drum, and age-0 white bass (*Morone chrysops*). These species were selected for analysis because they were the most prevalent in the diets of cormorants in Lake Erie (Bur *et al.* 1999). Although freshwater drum are benthic, gizzard shad, white bass, and emerald shiner are pelagic. Bottom trawl data typically underestimate the densities of pelagic fish species, relative to benthic species. However, bottom trawl data are most likely representative of spatial distribution of pelagic species.

The coordinates of the foraging flocks of cormorants located between 1 August 1999 and 1 September 1999 were mapped onto the contours of fish distribution. This time interval represented the trawling period for each year ± at least 10 days. Four size classes of cormorant flocks were considered in creating these maps: 1 to 10 individuals, 11 to 100 individuals, 101 to 1,000 individuals, and > 1,000 individuals. For each species of fish we used a Chi-square test (df = 1) for the null hypothesis that the proportions of foraging flocks in high- and low-catch regions were equal to the proportions of the catch regions' respective areas. Separate analyses were performed for three size classes of cormorant flocks: 1 to 10 individuals, 11 to 100 individuals, and > 100 individuals. Due to insufficient sample size, it was not possible to perform analyses on cormorant flocks with > 1,000 individuals.

RESULTS

Radiotelemetry

In 96 hr of tracking by boat and 24 hr of aerial tracking, 81 locations of foraging radio-tagged cormorants (Table 1, Fig. 2) were recorded. Distances from nearest shore for both aerial and surface tracking, and distances from Middle Island for surface

TABLE 1. Distances that radio-tagged cormorants were found from the nesting colony on Middle Island, Ontario and from the nearest shore, using aerial and surface telemetry. Data were collected between 1 July and 14 October 1999.

	Aerial (n = 39)	Surface (n = 42)
Distance from Middle Island (km)		
Mean (SD)	10.65 (7.77)	10.70 (3.68)
Median	11.2	11.4
Maximum	30.3	17.1
Distance from nearest shore (km)		
Mean (SD)	1.37 (0.83)	1.72 (1.27)
Median	1.1	1.3
Maximum	3.4	4.4

tracking were not normally distributed (Kolmogorov-Smirnov test, $P < 0.05$). Figure 2 suggests some spatial differences between the locations of individuals found by aerial and surface tracking. In particular, individuals found by surface tracking were located mainly east of Pelee Island and south of Kelley's Island. However, the median distances that radio-tagged birds were found from Middle Island with aerial and surface tracking, respectively,

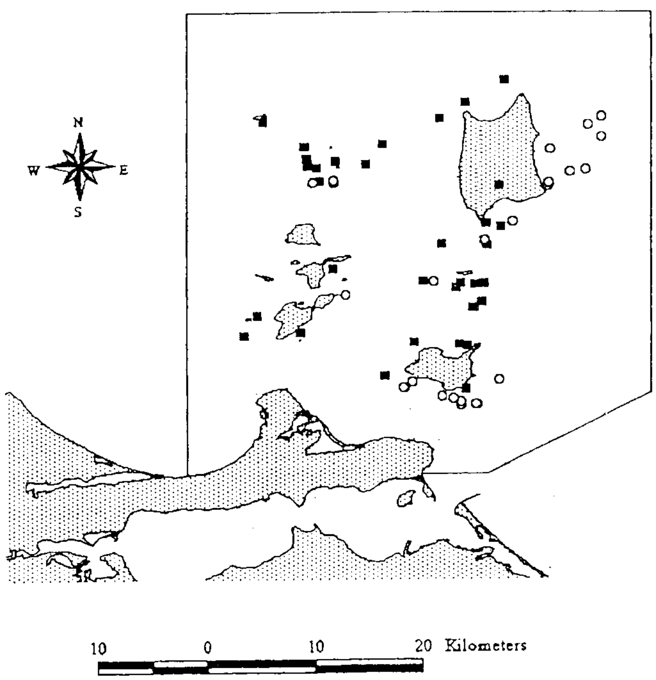


FIG. 2. Locations (n = 81) of foraging radio-tagged individual cormorants from surface (n = 42) and aerial (n = 39) observations. Symbols: ○ = individual found during surface observations, ■ = individual found during aerial surveys.

were not different (Kruskal-Wallis test, $\chi^2 = 0.027$, df = 1, $P = 0.870$). The maximal distances from Middle Island at which radio-tagged foraging cormorants were located during aerial and surface tracking were 30.3 km and 17.1 km, respectively (Table 1). These two observations are not shown in Figure 2 because they were outside of the study area. A greater maximum value was expected for aerial surveys because the entire study area was searched during each aerial survey, yet approximately one fourth of the study area was searched while conducting surface observations. However, the apparent spatial differences between the locations of radio-tagged individuals found by surface and aerial tracking could not be explained.

For radio-tagged cormorants located by surface tracking, the natural log of the distance from Middle Island did not change during the study period ($F_{1,40} = 0.290$, $P = 0.592$). For individuals located by aerial tracking, the natural log of the distance from Middle Island increased weakly during the study period ($F_{1,37} = 4.58$, $P = 0.039$, $r^2 = 0.110$). However, when the data (n = 3 observations) for the last date of aerial tracking (14 October) were removed, this trend did not exist ($F_{1,34} = 0.72$, $P = 0.401$). This result is consistent with the hypothesis that by 14 October, Middle Island may not have been the roost site of cormorants that bred there.

The median distances from nearest shore for aerial and surface observations were equal (Kruskal-Wallis test $\chi^2 = 2.13$, df = 1, $P = 0.338$). In all cases, foraging radio-tagged individuals were found within 5 km of shore. Approximately 79% (64 of 81) of the foraging radio-tagged cormorants located by aerial and surface tracking were within 2.5 km of shore. This represents a greater proportion of the radio-tagged cormorants that foraged within that distance than expected ($\chi^2 = 79.41$, df = 1, $P < 0.001$), based on the proportion of the study area (32.6%) that was within 2.5 km of shore.

Foraging Flocks: Depth, and Distance from Shore

There were 156 foraging flocks of cormorants recorded while conducting surface observations (Table 2, Fig. 3). Depths at which foraging radio-tagged cormorants were recorded were not different from those for flocks that did not contain radio-tagged individuals (Kruskal-Wallis test $\chi^2 = 2.00$, df = 1, $P = 0.400$). Therefore, the locations of flocks containing radio-tagged cormorants were combined with the locations of flocks that did not

TABLE 2. Number of flocks of cormorants observed during surface tracking (n = 156) in western Lake Erie, with respect to 2-m depth intervals, between 15 July and 28 September 1999.

Depth Interval (m)	Area (km²)	Flock Size 1–10	11–100	101–1,000	> 1,000	combined
0–2	27.513	1	1	0	0	2
2–4	35.793	5	4	3	1	13
4–6	94.216	3	6	2	7	18
6–8	182.769	17	9	6	2	34
8–10	372.591	31	22	9	3	65
10–12	376.545	9	11	0	0	20
12–14	103.936	1	1	1	0	3
14–16	3.499	1	0	0	0	1
Mean depth (m)		8.54	8.63	8.00	6.69	8.34
SD		2.43	2.60	2.57	1.97	2.51

in the analyses for depth. "Flock" size ranged from a single cormorant to an estimated 15,000 individuals. The mean depth of flocks with > 1,000 individuals was marginally less than that for the other classes of flock size (ANOVA, $F_{3,153} = 2.44$, $P = 0.067$). There was more error in estimating the center of flocks with > 1,000 individuals than the center of smaller flocks. Therefore, this difference in mean depth at which foraging cormorants were located may be an artifact of measurement error. All size classes of flocks were found more frequently than expected on water ≤ 10 m deep (Table 3). The combined set of flocks was found more frequently than expected, based on available area, on water ≤ 8 m deep. This result was probably due to flocks with 101 to 1,000 individuals and flocks with > 1,000 individuals both occurring more frequently

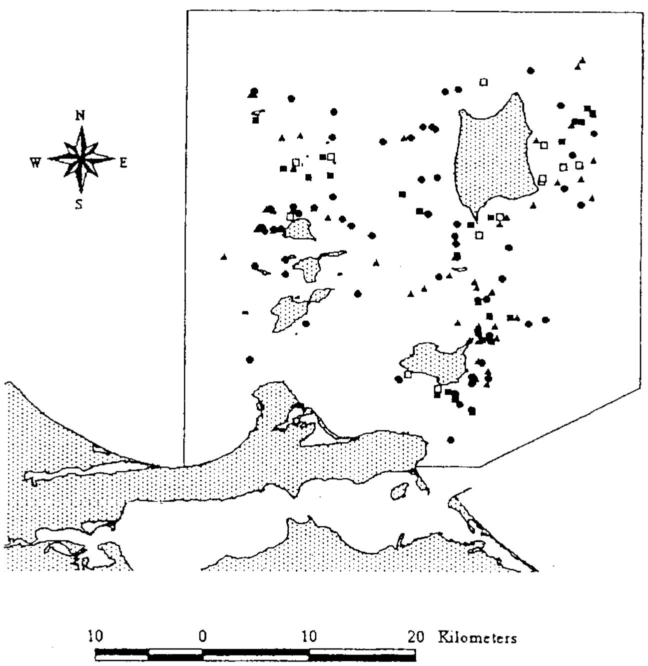


FIG. 3. Locations of foraging flocks (n = 156) of cormorants from surface observations. Symbols: ● = 1 to 10 individuals, ▲ = 11 to 100 individuals, ■ = 101 to 1,000 individuals, □ = > 1,000 individuals.

TABLE 3. Tests of the null hypothesis that foraging flocks (n = 156) of cormorants in western Lake Erie occurred proportionately equally, based on available area, in shallow and deep water. Separate tests were performed in which "shallow" water was defined as (1) depth ≤ 8m (28.4% of the water area) and (2) depth ≤ 10m (59.56% of the area of the water area). For the flock size class of > 1,000 individuals, probabilities were calculated with the binomial distribution. For the remaining size classes, the values of χ^2 (df = 1) are shown.

Flock Size Class	Criterion for shallow depth ≤ 8m	≤ 10m
1–10	3.21 +	16.62**
11–100	1.96 NS	7.44**
101–1,000	5.92*	11.02**
> 1,000	**	**
Combined	16.16**	40.65**

Symbols: + = $0.10 < P < 0.05$; * = $P < 0.05$; ** = $P < 0.01$; NS = $P > 0.10$

TABLE 4. Tests of the null hypothesis that foraging flocks of double-crested cormorants occurred proportionately equally, based on area of water within the study area that was 3.0 km (39.1% of the area) from shore, and 2.5 km from shore (32.6% of the area). For the flock size class of > 1,000 individuals, probabilities were calculated with the binomial distribution. For the remaining size classes, the values of χ^2 (df = 1) are shown.

Flock Size Class	n	Within 3 km of shore	χ^2	Within 2.5 km of shore	χ^2
1–10	68	58	60.94**	43	44.55**
11–100	54	43	37.25**	36	30.65**
101–1,000	21	13	4.59*	12	5.76*
>1,000	13	12	**	10	**
Combined	156	126	35.96**	101	140.62**

Symbols: * = $P < 0.05$, ** = $P < 0.01$

on water ≤ 8m deep. Flocks with 1 to 10 cormorants were found marginally more frequently ($0.10 < P < 0.05$) on water ≤ 8 m deep.

For flocks that did not contain radio-tagged cormorants, the median distance from nearest shore was not different from the median distance for the radio-tagged individuals found with surface tracking (Kruskal-Wallis test, $\chi^2 = 1.52$, df = 1, $P = 0.218$). Therefore, data for flocks containing radio-tagged individuals were combined with data for flocks that did not in the analyses of distance from nearest shore. Distances at which foraging flocks, irrespective of size, were recorded from nearest shore ranged from 0.6 km to 5.3 km. Approximately 80% (126 of 156) of the flocks occurred within 3.0 km of shore, and 65% (101 of 156) occurred within 2.5 km of shore. All flock size classes and the combined set of flocks foraged more than expected, based on area, in water within both 2.5 km and 3.0 km of shore (Table 4).

There was a weak and positive correlation between the number of foraging flocks, regardless of flock size, observed within 3 km of islands in the study area and $\log_e$ of the areas of those islands (Table 5, $F_{1,9} = 6.43$, $P = 0.035$, $r = 0.446$). There were no bivariate discordancies in either magnitude or trend for number of foraging flocks and $\log_e$ island area (Mardia's multivariate kurtosis, $b_{2,2} = 6.59$, $P = 0.43$). However, there was considerable variance in this association. For example, 8 flocks, 3 of which had more than 10 individuals, were found within 3 km of South Bass, Middle Bass,

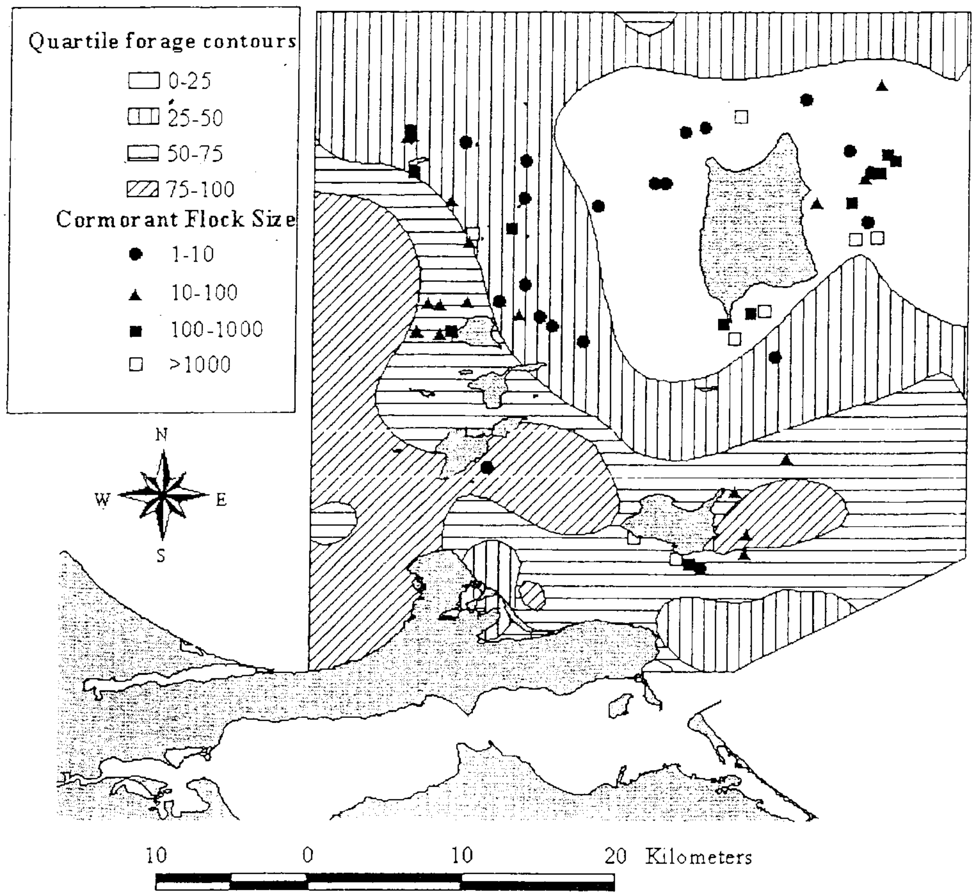
TABLE 5. Number of foraging flocks of cormorants recorded within 3 km of islands in the study area during surface tracking conducted between 15 July and 28 September 1999.

Island	Length of shoreline (km)	Island area (km²)	Foraging flocks
Pelee	34.433	40.907	37
Kelleys	18.343	11.319	30
South Bass	17.216	6.354	1
Middle Bass	12.389	3.290	3
North Bass	8.367	2.849	18
East Sister	1.609	0.263	5
Rattlesnake	2.574	0.243	2
Middle	1.448	0.210	8
Sugar	1.448	0.162	1
Hen	0.644	0.024	7
Green	1.287	0.069	1

Rattlesnake, Green, and Sugar islands. These islands are all within 4 km of each other, and their combined area is approximately 15% of the total island area considered in this study. In contrast, there were 20 flocks, 12 of which had more than 10 individuals, within 3 km of Hen Island, Middle Island, and East Sister Island. The combined area of these three islands is less than 1% of the total island area. This is marginally different ($\chi^2 = 3.20$, df = 1, $P = 0.07$) than expected for these two sets of islands, based on the relationship between number of foraging flocks within 3 km and $\log_e$ of island area observed in this study.

Spatial Associations Between Cormorants and Fish

There was considerable spatial variation in the historical distributions of the prey fishes (Figs. 4–7), but some similarities occurred in the locations of the regions containing highest historical catches (highest quartile regions in Figs. 4–7). For white bass, regions containing highest historical catches occurred between Kelleys and South Bass islands, east of Kelleys Island, and the in western and southwestern portions of the study area (Fig. 4). Freshwater drum were most abundant historically between Kelleys and South Bass islands, west of South Bass Island, and south and southeast of Kelleys Island (Fig. 5). Emerald shiners were most abundant west of the Bass Island group, and in the extreme northern and southeastern portions of the study area (Fig. 6). The lowest historical catches (lowest quartile) of emerald shiner, white bass, and

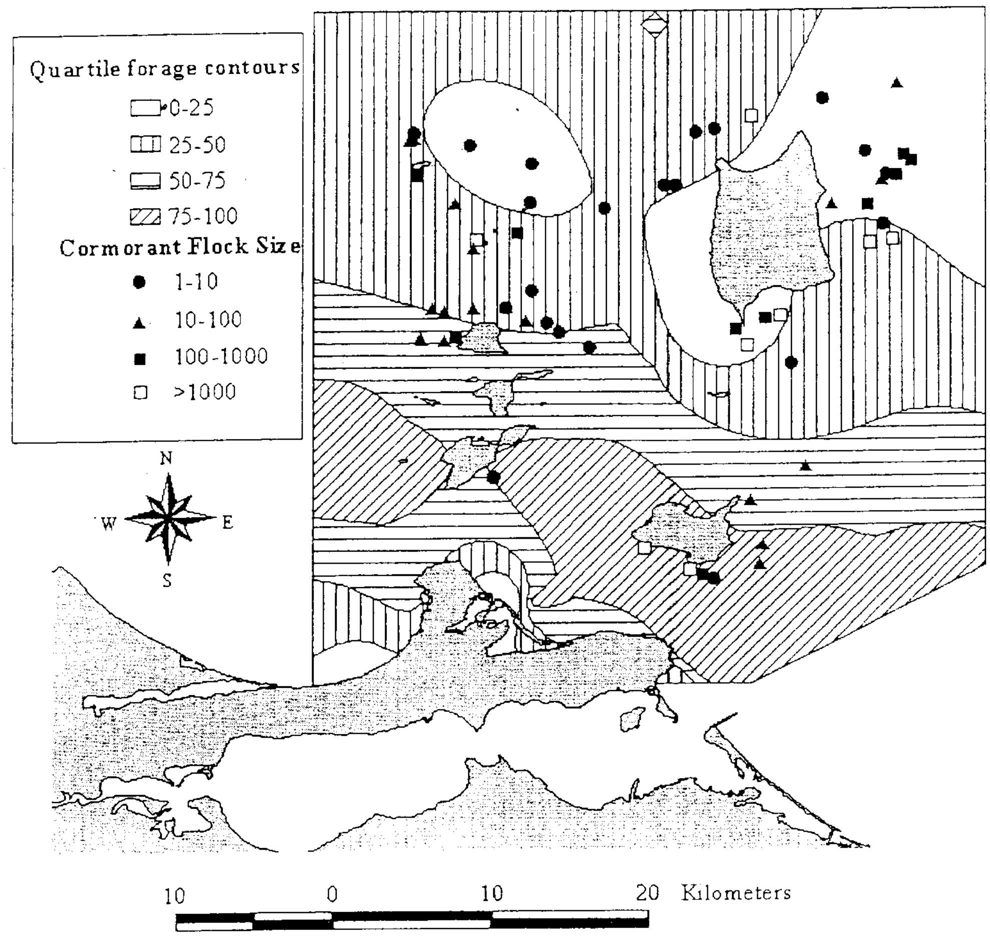


white bass

FIG. 4. Quartile contours for the geometric means of the percentage rank of catches of white bass and locations of foraging flocks of double-crested cormorants. Contours were generated from bottom trawl surveys conducted during August from 1988 through 1999. Locations of cormorant flocks were obtained from surveys conducted from 1 August through 1 September 1999. Symbols for cormorant flock sizes: ● = 1 to 10 individuals, ▲ = 11 to 100 individuals, ■ = 101 to 1,000 individuals, □ = > 1,000 individuals.

freshwater drum were mainly in the northeastern portion of the study area, around Pelee Island. Regions containing highest historical catches of gizzard shad occurred in the extreme western portions of the study area (Fig. 7). The lowest historical catches of gizzard shad occurred in the eastern part of the study area, and in the area south of Pelee Island.

The proportion of the study area resulting in historically high catches (geometric mean > median catch value) ranged from approximately 0.405 for freshwater drum to 0.550 for gizzard shad (Table 6). There were 58 flocks of foraging cormorants recorded between 1 August and 1 September 1999, including 21 flocks containing 1 to 10 individuals, 19 flocks containing 11 to 100 individuals, and 18 flocks containing > 100 individuals (Table 6). We rejected the null hypothesis that the proportions of flocks recorded were equal to the proportions of the catch regions' respective areas for six combinations of fish species and cormorant flock sizes: white bass for flocks of 1 to 10 and 11 to 100 individuals, emerald shiner for flocks with > 100 individuals, and gizzard shad for all three flock size classes ana-



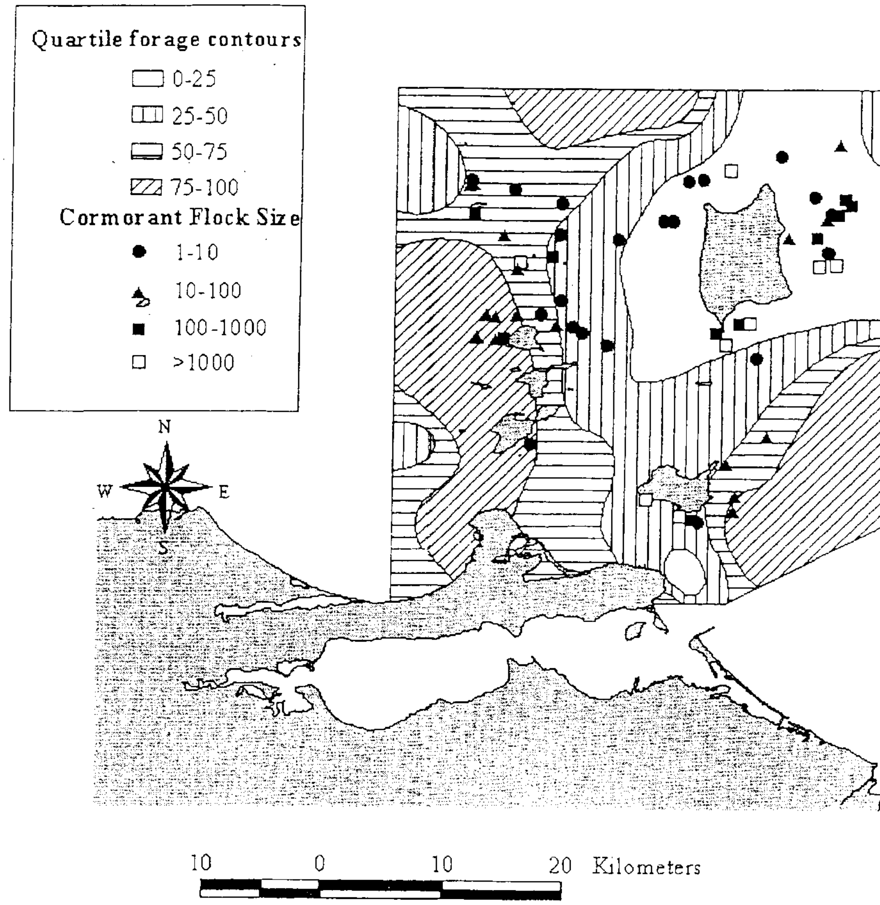
freshwater drum

FIG. 5. Quartile contours for the geometric means of the percentage rank of catches of freshwater drum and locations of foraging flocks of double-crested cormorants. Contours were generated from bottom trawl surveys conducted during August from 1988 through 1999. Locations of cormorant flocks were obtained from surveys conducted from 1 August through 1 September 1999. Symbols for cormorant flock sizes: ● = 1 to 10 individuals, ▲ = 11 to 100 individuals, ■ = 101 to 1,000 individuals, □ = > 1000 individuals.

lyzed. In all cases, however, rejection was due to a higher than expected number of flocks in regions that had historical catches that were lower than median (Table 6). Therefore, cormorants did not forage disproportionately more in areas that had higher than the historical median catches of prey fishes.

DISCUSSION

These results suggest that the most significant foraging pressure of cormorants on the fishery of the western basin of Lake Erie may be limited to areas within a 20-km radius of nesting colonies, within 3 km of shore, and in waters ≤ 10 m deep. These results agree with earlier studies that suggest that cormorants are highly selective in their feeding habitat. According to Mendall (1936), cormorants generally forage in water < 9 m deep. Palmer (1962) stated that cormorants forage over a wide range of depths, but typically less than 10 m. More than 80% of foraging flights observed by Custer

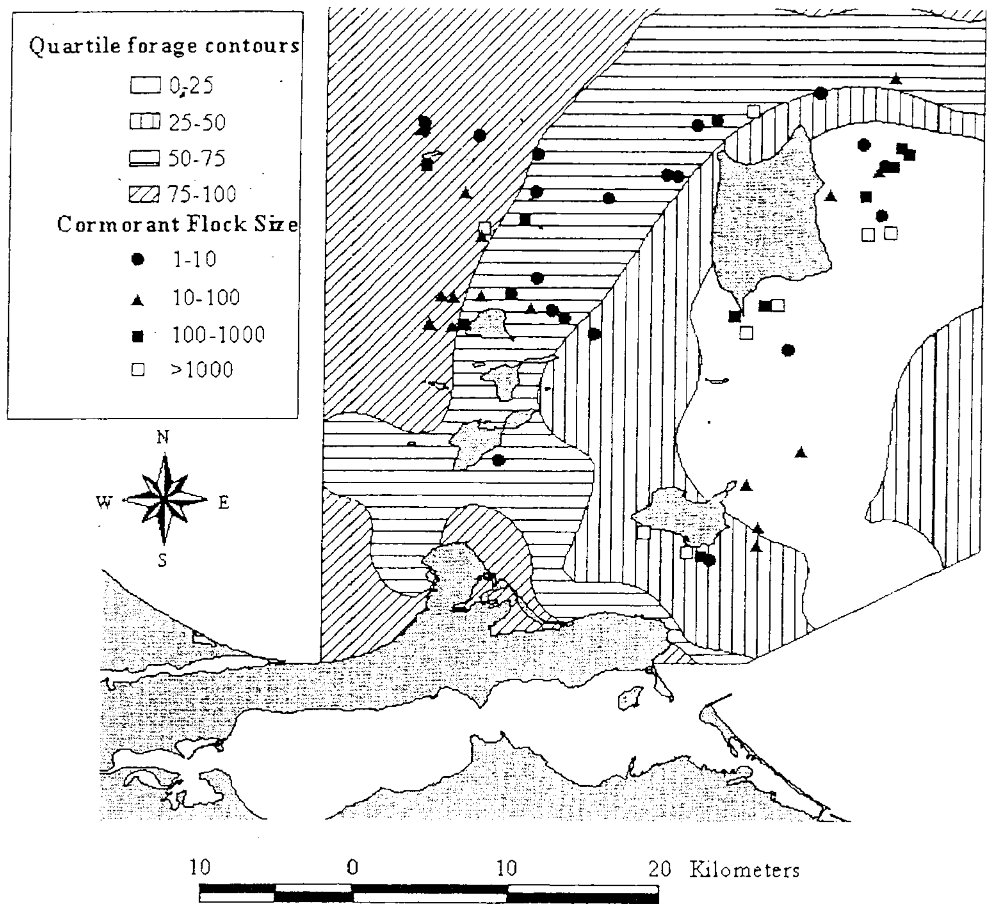


emerald shiner

FIG. 6. Quartile contours for the geometric means of the percentage rank of catches of emerald shiner and locations of foraging flocks of double-crested cormorants. Contours were generated from bottom trawl surveys conducted during August from 1988 through 1999. Locations of cormorant flocks were obtained from surveys conducted from 1 August through 1 September 1999. Symbols for cormorant flock sizes: ● = 1 to 10 individuals, ▲ = 11 to 100 individuals, ■ = 101 to 1,000 individuals, □ = > 1,000 individuals.

and Bunck (1992) were to waters < 9.1 m deep. Water depths ≥ 9.1 m were used less than expected within the maximum observed range for either colony studied by Custer and Bunck (1992). In this study, all size classes of flocks of foraging cormorants were found more frequently at depths of ≤ 10 m, similar to the findings of Custer and Bunck (1992), Palmer (1962), and Mendall (1936).

Individual nests were not monitored in this study. Therefore, it was not possible to determine the causes for the maximal distances from Middle Island from aerial and surface observations. However, radiotelemetric results of the foraging range of cormorants were comparable with prior studies. Palmer (1962) suggested that a requirement for nesting cormorants is an adequate food supply within approximately 16 km of the colony. Wanless *et al.* (1991, 1997) found that a congeneric species (*P. aristotelis*) utilized < 11% of the available habitat for foraging during chick rearing. The mean (SD) foraging distance found by Wanless *et al.* was 7.0 (1.9) km, with a maximum of 17 km from the



gizzard shad

FIG. 7. Quartile contours for the geometric means of the percentage rank of catches of gizzard shad and locations of foraging flocks of double-crested cormorants. Contours were generated from bottom trawl surveys conducted during August from 1988 through 1999. Locations of cormorant flocks were obtained from surveys conducted from 1 August through 1 September 1999. Symbols for cormorant flock sizes: ● = 1 to 10 individuals, ▲ = 11 to 100 individuals, ■ = 101 to 1,000 individuals, □ = > 1000 individuals.

colony. In this study, the mean foraging distance from the colony was approximately 10.7 km with a maximum distance of 30.3 km. Further, 79 of the 81 radio-tagged foraging cormorants were located within 19 km of Middle Island. The distance from the colony at which foraging cormorants were located did not change during the study period. Custer and Bunck (1992) recorded foraging flocks of cormorants at an average of 2.0 km and 2.4 km, respectively, from 2 breeding colonies in Green Bay on Lake Michigan, with a maximum of 40 km. Custer and Bunck's study was performed within 5 km of the mainland, along a peninsula, and there were numerous islands within 2 km of each other. These structural differences may have contributed to the shorter average distances from the colony recorded in that study. Custer and Bunck's locations also represented the first landing sites for the cormorants on each study date. The foraging locations found in this study were not necessarily the first for the cormorants on each day. However, the maximum range observed by Custer and Bunck (1992)

TABLE 6. Number of foraging flocks of cormorants found in regions of the study area that had historically high (greater than median) and low catches of four fish species during August in 1988 through 1999. The null hypothesis was tested for each species that the proportion of flocks found in high catch and low catch regions were equal to the regions' respective proportions of the study area (1,197 km²). The null hypothesis was tested with a Chi-square test (df = 1). Separate tests were conducted for 3 flock size classes.

	Proportion of study area			Number (proportion) of cormorant flocks in			
Fish species	High catch	Low catch	Flock size	High catch region	Low catch region	χ^2	P
white bass	0.421	0.579	1–10	2 (0.095)	19 (0.905)	7.76	< 0.01
			11–100	10 (0.526)	9 (0.473)	0.95	> 0.25
			> 100	4 (0.222)	14 (0.778)	2.60	0.111
freshwater drum	0.405	0.595	1–10	4 (0.190)	17 (0.810)	3.58	0.062
			11–100	7 (0.368)	12 (0.632)	0.10	0.750
			> 100	4 (0.222)	14 (0.778)	2.26	0.149
emerald shiner	0.519	0.481	1–10	14 (0.667)	7 (0.333)	1.38	0.244
			11–100	13 (0.684)	6 (0.316)	1.71	0.208
			> 100	5 (0.278)	13 (0.722)	4.27	0.041
gizzard shad	0.550	0.450	1–10	5 (0.238)	16 (0.762)	5.37	0.022
			11–100	3 (0.158)	16 (0.842)	7.72	< 0.01
			> 100	3 (0.167)	15 (0.833)	6.99	< 0.01

was less than that from this study. Finally, Custer and Bunck's study did not include data for the premigration and migration seasons.

These data suggest that the cormorants selected foraging areas near certain islands in the study area, and the number of foraging flocks found offshore was largely a function of island area. However, certain islands had disproportionately more flocks than expected, based on area. East Sister Island and Middle Island contained large colonies (> 3,400 nests in 1999 [Weseloh *et al.* 2002]) of nesting cormorants. Thousands of cormorants nesting on Middle Island and East Sister Island use Big Chicken Island, a small (area = 0.004 km²) treeless islet, as a loafing area during the day and as a roosting area during the night (M. Stapanian and M. Bur, USGS, unpublished data). Hen Island is approximately 2.5 km from Big Chicken Island. The proximity to both East Sister Island and to Big Chicken Island is probably one reason why a disproportionately large number of foraging flocks, based on island area, were recorded within 3 km of Hen Island. It is unclear why marginally fewer flocks were found within 3 km of South Bass, Middle Bass, Rattlesnake, and Sugar islands. Distance was not a factor because these islands are closer to Middle Island than to either Big Chicken or Hen islands. Differences in shoreline type and amount of boat traffic may have contributed to these differences. Unlike Middle and Big Chicken islands, the shorelines of South Bass, Middle Bass, Rattlesnake, and Sugar islands have visual evidence of development by humans. Further, a disproportionate amount of the boat traffic in the study area occurred within 1 km of developed shorelines (Stapanian and Bur 2002).

These results are consistent with those of Stapanian and Bur (2002), who found that the number of foraging cormorants was greatest offshore of the breeding colonies and loafing/roosting areas in the study area and least in open waters (depth 10 to 12 m, and distance from shore 2.8 to 8.6 km). In that study, however, there was no difference in the number of cormorants recorded on reefs and shoals and offshore of islands that had visual evidence of development by humans. Unlike the present study, Stapanian and Bur (2002) sampled the study area along established transects of standard length in specific habitats. These differences in methodology may in part account for the differences in results.

When the data for the last date of aerial tracking (14 October) were excluded, no temporal differences were found in the distance from the colony at which foraging radio-tagged cormorants were found. Further, it was not possible to determine if the spatial distribution of flocks recorded between 1 August and 1 September differed from any other time period. For management purposes, however, the time interval examined is instructive and conservative in understanding the impact on the fishery of the area. The number of foraging cormorants in the study area was higher during this period than during early summer because first-year birds were foraging by 1 August.

The results of this study strongly suggest that cormorants did not selectively forage within regions of the study area that had historically higher than median concentrations of prey fish species during the month of August. The statistical results suggesting that the cormorants foraged proportionately less in the regions containing catches that were higher than the historical median for certain species may be spurious. The relationship between the distribution of marine birds and their prey has been shown to be dependent on the spatial scale of ocean considered (Schneider and Duffy 1985, Schneider and Piatt 1986, Hunt and Schneider 1987, Hunt 1991). These studies suggest that the spatial association between the biomass of marine birds counted on transects and the biomass of their prey is much stronger over hundreds of square km of ocean than for single transect segments that are a few km in length. Perhaps the lack of association at the transect scale is in part due to avoidance of the boat and its equipment by fish as the boat approaches flocks of feeding seabirds. Use of 12 years of data from established trawling sites circumvented this potential problem. In this study, the scale was relatively large (1,197 km^2 of water). The results suggested that even at this scale there does not appear to be an association between the locations of cormorant foraging and the distribution of prey fish. Other studies (Obst 1985, Hunt 1991) suggest that marine birds may not always forage in the patches that contain the highest concentrations of prey, but that they forage in those ocean habitats having an average density of prey that is sufficient for their needs. The results of this study, coupled with the cormorants' rapid increase in population in the region over the last 20 years, support this latter hypothesis as applied to cormorants in western Lake Erie. It appears that the foraging locations of cormorants in western Lake Erie are based much more on distance from shore and depth than on the distributions of the four fish species most commonly eaten by cormorants.

A caveat in these results concerns the nature of the bottom trawling survey and bottom type. The majority of the nearshore areas (depth ≤ 3 m, representing < 5% of the study area) around most of the islands were classified as untrawlable. Nearshore areas in Lake Erie have historically been undersampled due to constraints associated with the typical sampling gear. Therefore, the contours of fish abundance may not have represented a true picture of abundance in areas that had depths ≤ 3 m. Although recent initiatives have identified the nearshore areas of the Great Lakes as important to ecosystem dynamics, there is a need for further information (Koonce *et al.* 1999). Further study should include an analysis of the spatial distributions of foraging flocks at various time intervals and data from midwater trawls.

Clearly, foraging effects of cormorants on the fishery of the Laurentian Great Lakes is an important aspect of managing this species. Based strictly on the results of this study and others concerning the effects of cormorants on the fishery of western Lake Erie (Madenjian and Gabrey 1995, Bur *et al.* 1999), there appears to be no need for population control of cormorants in the area at this time. Concern over impacts of cormorants on the forage fish base in Lake Erie is greatest in fall, when there is greatest overlap in the diets of cormorants and walleye (Bur *et al.* 1999). Fall is also the time in which migratory waterbirds such as cormorants and red-breasted mergansers (*Mergus serrator*) use western Lake Erie as a resting and feeding area. A bioenergetics model (Madenjian and Gabrey 1995) indicated that all species of waterbirds combined consumed approximately 15.2% of the prey biomass that supports walleye populations in western Lake Erie for a single growing season. However, predation by cormorants on fish accounted for only 1.7% of the biomass that supports walleyes for 1 year. Madenjian and Gabrey (1995) predicted that even if the nesting population of cormorants doubled, the predation on forage fish would increase only modestly. At present the impact of cormorants on the fishery of western Lake Erie appears to be localized and minimal.

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